MOLECULAR PHYLOGENETIC RELATIONSHIPS AMONG THE WOOD WARBLERS (PARULIDAE) AND HISTORICAL BIOGEOGRAPHY IN THE CARIBBEAN BASIN

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Abstract.—Although diversification and adaptive radiation of birds on archipelagoes have served as exemplars of the evolutionary process, prior attention has focused on the avifauna of the Hawaiian and Galapagos Islands, with little attention paid to West Indian species. One group of birds that includes several Caribbean endemics is the family of Wood Warblers (Passeriformes: Parulidae). This family contains some of the best-studied avian species in North America, lacking only an historical context for comparing behavior and ecology of the species. A phylogeny for this group would also provide an objective basis for inferring the evolutionary origins of some of the endemic West Indian bird species. In this paper we present the results of a phylogenetic analysis of relationships among parulid genera and species using DNA sequences (1140 base pairs) from the mitochondrial cytochrome *b* gene. Results of this study indicate that the family Parulidae is not monophyletic. Perhaps the most significant finding is that many of the currently recognized genera are also not monophyletic. These include *Dendroica*, *Seiurus*, *Vermivora*, *Wilsonia*, and *Parula*. Also of significance is the evidence found that morphologically divergent species in this region represent previously unrecognized adaptive radiations. Finally, we identify the first example of intra-island adaptive radiation proposed for any of the West Indian avifauna. This involves a well-supported clade in Hispaniola, including the Black-crowned Palm-Tanager (*Phaenicophilus palmarum*), the Green-tailed Warbler (*Microligea palustris*), and the White-winged Warbler (*Xenoligea montana*). Evidence of intra-island adaptive radiation has important implications for understanding historical biogeography of the Caribbean region.

Key words: *biogeography*, *Caribbean Basin*, *Parulidae*, *phylogeny*, *wood warbler*

Resumen.—RELACIONES MOLECULARES FILOGENÉTICAS ENTRE LAS REINITAS DE BOSQUE (PARULIDAE) Y BIOGEOGRAFÍA HISTÓRICA EN LA CUENCA DEL CARIBE. Aunque la diversificación y la radiación adaptiva de las aves en los archipiélagos han servido como ejemplos del proceso evolutivo, previamente la atención se ha centrado en la avifauna de las islas Hawai y las Galápagos, con poca atención prestada a las especies de las Indias Occidentales. Un grupo de aves que incluye varios endemismos caribeños es la familia de las reinitas de bosque (Passeriformes: Parulidae). Esta familia contiene algunas de las especies mejor estudiadas en América del Norte, careciendo solamente de un contexto histórico para comparar el comportamiento y la ecología de las especies. Una filogenia para este grupo también proporcionaría una base objetiva para deducir los orígenes evolutivos de algunas de las especies de aves endémicas a las Indias Occidentales. En este trabajo presentamos los resultados de un análisis filogenético de las relaciones entre géneros y especies de parúlidos usando secuencias de ADN (1140 bases pares) del gen del citocromo *b* mitocondrial. Los resultados de este estudio indican que la familia Parulidae no es monofilética. Quizás el hallazgo más significativo es que muchos de los géneros actualmente reconocidos tampoco son monofiléticos. Éstos incluyen *Dendroica*, *Seiurus, Vermivora, Wilsonia* y *Parula*. También de importancia es la evidencia que indica que las especies morfológicamente divergentes en esta región representan radiaciones adaptivas previamente desconocidas. Finalmente, identificamos el primer ejemplo de radiación adaptiva intra-isla jamás propuesto para cualquier avifauna de las Indias Occidentales, un clado bien respaldado por datos en La Española con la Tangara Palmera Coroninegra *(Phaenicophilus palmarum)*, la Reinita Coliverde *(Microligea palustris)*, y la Reinita Aliblanca *(Xenoligea montana).* La evidencia de la radiación adaptiva intra-isla tiene implicaciones importantes para entender la biogeografía histórica de la región del Caribe.

Palabras clave: *biogeografía*, *cuenca del Caribe*, *filogenia*, *Parulidae*, *reinita de bosque*

Résumé.—PHYLOGÉNIE MOLÉCULAIRE CHEZ LES PARULINES (PARULIDAE) ET BIOGÉOGRAPHIE HISTORIQUE DANS LE BASSIN CARAÏBE. Bien que la diversification et la radiation adaptative des oiseaux dans les archipels aient servi d'exemple pour la compréhension des processus d'évolution, l'attention s'est jusqu'à présent portée sur l'avifaune des îles Hawaii et des Galapagos, avec peu d'intérêt pour les espèces des Antilles. La famille des parulines (Passériformes : Parulidae) est un groupe d'oiseaux qui comporte plusieurs espèces endémiques caraïbe. Elle comporte certaines des espèces d'oiseaux les mieux connues d'Amérique du Nord, manquant juste de mise en perspective du contexte historique pour comparer leur comportement et leur écologie. Une phylogénie de ce groupe donnerait une base objective pour traiter des origines évolutives de certaines espèces endémiques des Caraïbes. Nous présentons ici les résultats d'une analyse phylogénétique des relations entre les genres et les espèces de parulines en utilisant le séquençage de l'ADN (1140 paires de bases) du gène du cytochrome *b*. Les résultats indiquent que la famille Parulidae n'est pas monophylétique. Le résultat peut-être le plus significatif est que beaucoup des genres actuellement reconnus ne le sont pas non plus. Ceux-ci comportent les genres *Dendroica, Seiurus, Vermivora, Wilsonia* et *Parula*. Un autre résultat d'importance est qu'il a été trouvé que des espèces morphologiquement divergentes de la région représentent des radiations adaptatives auparavant non reconnues. Enfin, nous avons identifié le premier exemple de radiation adaptative intra île proposée pour une espèce d'oiseaux. Il s'agit d'un clade bien caractérisé à Hispaniola qui comprend le Tangara à couronne noire (*Phaenicophilus palmarum*), la Paruline aux yeux rouges (*Microligea palustris*) et la Paruline à ailes blanches (*Xenoligea montana*). La démonstration de radiation adaptative intra insulaire a d'importantes répercussions pour comprendre l'histoire de la biogéographie de la région caraïbe.

Mots-clés: *biogéographie*, *bassin caraïbe*, *Parulidae*, *phylogénie*, *parulines*

THE AVIFAUNA of the West Indian archipelago includes many single island endemics, Caribbean endemics found on multiple islands, as well as species with more widespread distributions that include continental areas. Diversification and adaptive radiation of birds on archipelagoes have served as exemplars of the evolutionary process. However, prior attention has mainly been focused on the avifauna of the Hawaiian and Galapagos Islands. The *in situ* evolution of some endemic Caribbean species (i.e., from other West Indian birds), as well as the possibility that some mainland species may in fact be derived from West Indian taxa, has seldom been considered. This is in spite of well-documented Caribbean radiations in *Anolis* lizards and some other taxonomic groups (Hedges *et al.* 1994, Hedges 1996, Losos *et al.* 1998). The Caribbean avifauna has been assumed to owe its origins to dispersal from continental areas (Bond 1963, 1978; Pregill and Olson 1981), or from vicariant events (Rosen 1976) with the closest relatives of individual endemic island taxa thought to be continental forms (Bond 1963, 1978; Ricklefs and Cox 1972). Until recently, the origin of West Indian birds was inferred without objective analysis (Bond 1963, 1978), or was based on assumptions of evolutionary processes (Ricklefs and Cox 1972). As modern systematic methodologies and molecular data have become more commonly used, the origin and relationships of Caribbean birds can now be more rigorously assessed (Klein and Brown 1994, Seutin *et al.* 1994, Hunt *et al.* 2001, Lovette and Bermingham 2001).

One group of birds that includes several Caribbean endemics is the family of wood warblers (Passeriformes: Parulidae). Wood warblers are mainly insectivorous New World species that vary markedly in plumage color pattern and vocalizations, but exhibit relatively little variation in bill morphology. The family has a wide distribution, with representatives from Alaska to southern South America. It contains some of the best-studied avian species in North America. Research on parulid foraging ecology, singing and courtship behavior, nest success, and non-breeding season ecology has been critical in the development of modern ideas in ecology, evolution, behavior, and conservation (MacArthur 1958, Ficken and Ficken 1962a, Burtt 1986, Morse 1989, Shutler and Weatherhead 1990, Spector 1992, Martin and Badyaev 1996). What has been lacking for the group is the historical context provided by a hypothesis of phylogenetic relationships. In addition, a phylogeny would provide an objective basis for inferring the evolutionary origins of some of the endemic West Indian bird species. It would also allow reexamination and reinterpretation of prior work on the evolution of plumage color patterns (Burtt 1986), sexual selection (Shutler and Weatherhead 1990), and singing and courtship behavior (Ficken and Ficken 1962a, Spector 1992).

Parulidae is part of an assemblage of New World bird groups, the members of which all have only a vestigial tenth primary (they are the so-called "nine-primaried oscines"). Because of this feature, they have all been assumed to be closely related (Raikow 1978). This group consists of members of the families Vireonidae, Peucedramidae, Parulidae, Coerebidae, Thraupidae, Emberizidae, Cardinalidae, Icteridae, and Fringillidae. Only recently has the Vireonidae been demonstrated to not be closely related to the others (Sibley and Ahlquist 1990, Cicero and Johnson 2001). Whether the remaining families comprise a monophyletic group remains to be determined. The relationships among nine-primaried oscine families, as well as their individual taxonomic limits, have been investigated with both molecular and morphological data (Raikow 1978, Bledsoe 1988, Sibley and Ahlquist 1990, Klicka *et al.* 2000, Sato *et al.* 2001), but with little consensus among studies. The sister taxon to the parulids is thus still not conclusively identified, nor has monophyly of the family been demonstrated.

Many questions also remain regarding the relationships of different species and genera of parulids. Although recent analyses of relationships within the genera *Dendroica* (Lovette and Bermingham 1999) and *Parula* (Lovette and Bermingham 2001) exist, the only general systematic treatments of the Parulidae have included relatively few of the 115 species and 26 genera as the goals of these studies were often broader in scope than the phylogeny of Parulidae (e.g., Raikow 1978, Avise *et al*. 1980, Bledsoe 1988, Sibley and Ahlquist 1990).

In this paper we present the results of a phylogenetic analysis of relationships among parulid genera and species using DNA sequences (1140 base pairs) from the mitochondrial cytochrome *b* gene. Using the phylogenies generated in this study, we address 1) monophyly of Parulidae as currently defined, 2) the monophyly of selected parulid genera, 3) taxonomic and phylogenetic implications, and 4) implication for the historical biogeography of the Caribbean.

METHODS

Taxon Sampling and Outgroups

For consistency, taxonomy and species names used in this paper follow the American Ornithologists' Union (1998) Check-list. Nineteen of the 26 genera currently recognized as belonging to Parulidae were sequenced. Because of the potential problems associated with representing a genus by only one species, individuals from at least two species were used for all non-monotypic genera. More than one conspecific individual was also included for several species in order to have better geographical representation. In addition to these warblers, we also included the Bananaquit (*Coereba flaveola*) and a representative of the emberizid genus *Conirostrum*. We included these taxa because they have been previously considered closely related to warblers. In addition, we also included three genera of tanagers (*Chlorospingus*, *Spindalis*, and *Phaenicophilus*) based on plumage similarities among these species and the Hispaniolan endemic warblers *Microligea* and *Xenoligea* (McDonald 1988; R. W. Storer, pers comm.). Trees were rooted using a representative of the blackbird family Icteridae (*Icterus dominicensis*). Most of these sequences are new to this study (GenBank accession numbers AY216801–AY216867), but a few have already been published (Burns 1997: AF006218; Burns *et al.* 2002: AF489881, AF489883, AF489891, AF489894).

Voucher specimens were prepared as museum study skins, skeletons, or skin and skeleton combinations and deposited in museum collections (Table 1). Due to legislation with no provision for scientific collecting in the Cayman Islands, voucher specimens do not exist for *Dendroica vitellina.* For all vouchered specimens, either total DNA extracts or purified mtDNA (Table 1) were prepared from heart, liver, or pectoral muscle tissue preserved in liquid nitrogen or in "Queen's" buffer (Seutin *et al.* 1991), and stored at -80°C. Total DNA was extracted from cells remaining in the base of a remige removed from a color-banded individual of *D. vitellina* and subsequently stored in "Queen's" buffer. All total DNA extractions were done with a 5% Chelex solution (Walsh *et al.* 1991). Mitochondrial DNA was isolated and purified from tissues of many of the specimens according to methods outlined in Klein and Brown (1994). To lower the probability that nuclear copies were being analyzed, both strands were sequenced, initial amplification was of large fragments, overlapping internal fragments were sequenced, more than one individual was sequenced for most genera, and purified mtDNA was the DNA source for many taxa. The sequences derived from total DNA did not differ in any significant way from those derived from purified mtDNA. Large fragments of cytochrome *b* were amplified on an air thermal cycler using PCR with the following primers: H15915 (Helm-Bychowski and Cracraft 1993), L15308, H15710, and L14851 (Groth 1998). Typical initial double-stranded amplification protocols (10 ul volumes) were 37 cycles of 94°C: 2 seconds, 48°C: 0 seconds, and 70°C: 25 seconds. Using internal primers, shorter fragments were then amplified from the initial PCR product using H15915, L15656, H15710, L15308, H15505, L16206, H15298, and L14851 (Groth 1998) at a higher annealing temperature (55°C). Double-stranded PCR products were then cleaned and cycle sequenced (ABI Prism™ Dye Terminator Cycle Sequencing Ready Reaction kit with AmpliTaq DNA Polymerase, FS; Perkin Elmer) using this protocol: 96°C: 1 minute; then 32 cycles of 96°C: 10 seconds; 50°C: 5 seconds; 60°C: 3 minutes. Samples were run on polyacrylamide gels on an ABI Prism™ 377.

Phylogenetic analyses

Phylogenetic trees were generated using both parsimony and Bayesian approaches. Parsimony analyses were performed using PAUP* 4.0b8 (Swofford 2001) under two different weighting schemes. Trees were initially generated by weighting all characters equally. However, plots of total percent sequence divergence versus divergence at first, second, and third position sites indicate that third position sites

Table 1. Species names, museum, and voucher numbers of individuals included in this study. AMNH = American Museum of Natural History; ANSP = Academy of Natural Sciences Philadelphia; FLS = Fundacion La Salle, Venezuela; FMNH = Field Musem of Natural History; MVZ = Museum of Vertebrate Zoology, University of California at Berkeley; UNAM = Universidad Nacional Autonoma de México; MNCR = Museo Nacional, Costa Rica; UMMZ = University of Michigan Museum of Zoology.

Scientific name	Common name	Museum and voucher number
Basileuterus rufifrons	Rufous-capped Warbler	MNCR NKK244
Basileuterus tristriatus	Three-striped Warbler	UMMZ 227798
Cardellina rubrifons	Red-faced Warbler	LSUMNS B-10178
Chlorospingus pileatus	Sooty-capped Bush-Tanager	LSUMNS B-19947
Coereba flaveola	Bananaquit	UMMZ 225179
Conirostrum bicolor	Bicolored Conebill	UMMZ 227715
Dendroica adelaidae	Adelaide’s Warbler	LSUMNS B11431
Dendroica angelae	Elfin-woods Warbler	LSUMNS B11459
Dendroica caerulescens	Black-throated Blue Warbler	UMMZ 232197
Dendroica castanea	Bay-breasted Warbler	NKK571
Dendroica discolor 1	Prairie Warbler	UMMZ 227213
Dendroica discolor 2	Prairie Warbler	AMNH NKK802
Dendroica dominica	Yellow-throated Warbler	AMNH NKK869
Dendroica magnolia	Magnolia Warbler	UMMZ 227690
Dendroica palmarum	Palm Warbler	NKK321
Dendroica pensylvanica	Chestnut-sided Warbler	UMMZ 231694
Dendroica petechia 1	Yellow Warbler	UMMZ NKK302
Dendroica petechia 2	Yellow Warbler	UMMZ NKK490
Dendroica pharetra	Arrowhead Warbler	FMNH 331126
Dendroica pinus 1	Pine Warbler	AMNH BD963
Dendroica pinus 2	Pine Warbler	AMNH NKK905
Dendroica pinus 3	Pine Warbler	AMNH JAG2164
Dendroica striata	Blackpoll Warbler	UMMZ 227599
Dendroica virens	Black-throated Green Warbler	UMMZ NK541
Dendroica vitellina	Vitelline Warbler	AMNH NKK755
Geothlypis speciosa	Black-polled Yellowthroat	AMNH PEP1901
Geothlypis trichas	Common Yellowthroat	UMMZ 227795
Helmitheros vermivorus	Worm-eating Warbler	UMMZ 231699
Icteria virens	Yellow-breasted Chat	LSUMNS B3326
Icterus dominicensis	Greater Antillean Oriole	AMNH NKK1112
Limnothlypis swainsonii	Swainson’s Warbler	UMMZ 231701
Microligea palustris 1	Green-tailed Warbler	AMNH
Microligea palustris 2	Green-tailed Warbler	AMNH NKK1055
Mniotilta varia	Black-and-white Warbler	881215
Myioborus albifacies	White-faced Whitestart	AMNH ML471
Myioborus brunneiceps	Brown-capped Whitestart	AMNH PRS453
Oporornis agilis	Connecticut Warbler	NKK570
Oporornis formosus	Kentucky Warbler	NKK125
Parula americana	Northern Parula	UMMZ 228374
Parula gutturalis 1	Flame-throated Warbler	LSUMNS B19935
Parula gutturalis 2	Flame-throated Warbler	LSUMNS B19898
Parula pitiayumi	Tropical Parula	LSUMNS B18571
Parula superciliosa 1	Crescent-chested Warbler	LSUMNS BMM040
Parula superciliosa 2	Crescent-chested Warbler	154
Phaenicophilus palmarum	Black-crowned Palm-Tanager	AMNH 831246
Protonotaria citrea	Prothonotary Warbler	FLS NKK505
Seiurus aurocapillus	Ovenbird	881216
Seiurus motacilla	Louisiana Waterthrush	LSUMNS B16861
Setophaga ruticilla	American Redstart	UMMZ NKK293

Table 1 (concluded).

Scientific name	Common name	Museum and voucher number
Spindalis zena	Western Spindalis	AMNH NKK862
Teretistris fernandinae	Yellow-headed Warbler	ANSP 186515
Vermivora celata 1	Orange-crowned Warbler	LSUMNS B19168
Vermivora celata 2	Orange-crowned Warbler	LSUMNS B19692
Vermivora chrysoptera 1	Golden-winged Warbler	ANSP 183700
Vermivora chrysoptera 2	Golden-winged Warbler	ANSP 183677
Vermivora crissalis	Colima Warbler	LSUMNS 95L
Vermivora luciae 1	Lucy's Warbler	LSUMNS B23331
Vermivora luciae 2	Lucy's Warbler	LSUMNS B23332
Vermivora peregrina 1	Tennessee Warbler	FLS 89-1264
Vermivora peregrina 2	Tennessee Warbler	FMNH
Vermivora pinus 1	Blue-winged Warbler	ANSP 183679
Vermivora pinus 2	Blue-winged Warbler	ANSP 183682
Vermivora ruficapilla 1	Nashville Warbler	89-303
Vermivora ruficapilla 2	Nashville Warbler	B20694
Vermivora ruficapilla 3	Nashville Warbler	MVZ 173509
Vermivora ruficapilla 4	Nashville Warbler	MVZ 173510
Vermivora virginiae 1	Virginia's Warbler	CMM110
Vermivora virginiae 2	Virginia's Warbler	CMM098
Wilsonia canadensis	Canada Warbler	UMMZ 231702
Wilsonia citrina	Hooded Warbler	LSUMNS B856
Wilsonia pusilla	Wilson's Warbler	LSUMNS B23419
Xenoligea montana	White-winged Warbler	AMNH NKK1041

may be saturated for transitions. Therefore, we also performed an additional parsimony analysis in which we downweighted third position transitions by a factor of seven. This was accomplished by giving third position transitions a weight of one and all other characters a weight of seven using the stepmatrix option in PAUP. The ratio of 7:1 was obtained empirically from examining multiple sequences for each of two of the larger genera used in this study: *Vermivora* and *Dendroica*. We chose to estimate the transition/transversion ratio among close relatives because close relatives will have fewer multiple substitutions at a given site than more distant relatives. Thus, the ratio of 7:1 is probably a more accurate estimate of the actual transition bias than the ratio observed among all species included in the study (Edwards 1997). Both parsimony analyses consisted of heuristic searches of 1000 random addition sequences each. To estimate support for different nodes, both parsimony analyses were bootstrapped with 10 random addition replicates per each of 1000 bootstrap replicates.

Phylogenetic relationships were also explored using a Bayesian approach. For this analysis, we first chose a best-fit model of evolution using Modeltest, vers. 3.06 (Posada and Crandall 1998). We then used the chosen model (GTR + I + gamma) in conjunction with MrBayes 2.01 (Huelsenbeck and Ronquist 2001) to perform Bayesian analyses on the data set. Parameters of the GTR + I + gamma model were treated as unknown variables with uniform prior values and estimated as part of the analysis. The analysis was run for 1,000,000 generations and sampled every 100 generations. Thus, the analysis resulted in 10,000 samples. Four Markov Chain Monte Carlo chains were run for each analysis. Resulting log likelihood scores were plotted against generation time to identify the point at which log likelihood values reached a stable equilibrium value. Sample points prior to this point of stationarity were discarded as "burn-in" samples. The remaining samples were used to produce a majority rule consensus tree with the percentage values indicating the percentage of samples that identified a particular clade (the clade's posterior probability). These posterior probability values provide a measure of support for a particular clade.

RESULTS

Sequence variation

Typical of cytochrome *b* sequences, mean proportions of the four nucleotides were unequal (A = 0.28, G = 0.35, C = 0.13, T = 0.24; Chi-square test for homogeneity of base frequencies across taxa ignoring correlations due to phylogenetic structure P = 1.0). All differences between taxa were base substitutions; no insertions or deletions were detected. Of the 450 variable nucleotide sites, 381 were phylogenetically informative. As expected, transitions greatly outnumbered transversions at all positions.

Pairwise percent divergence within species was generally low (mean 0.86%), but differences between subspecies of Yellow Warbler (2.1%) and of Nashville Warbler (mean 2.0%) were on the order of (or even greater than) divergences seen between some well-recognized species (e.g., *Parula americana* and *P. pitiayumi*: 1.2%, and *Dendroica castanea and D. striata*: 1.8%). Divergence between parulid species ranged widely (1.0–12.4%, mean 8.1%). Some clades identified in the tree had much lower interspecific divergences than did others, indicating disparate timings of diversification of major groups. For example, mean pairwise divergence within the clade of mainly southwestern *Vermivora* was 2.0%, whereas divergence levels among *Dendroica* warblers was 6.3%. Sequence divergence within the clade of the *Phaenicophilus* tanager and its warbler-like sister species (see below) averaged 9.3%.

Phylogenetic relationships

The equally weighted analysis resulted in 178 most parsimonious trees, each with 2427 steps and a consistency index (excluding uninformative characters) of 0.2529. A strict consensus of these 178 trees (Fig. 1) is resolved at basal and more recent clades. However, the trees disagree in the placement of intermediate clades. The 7:1 weighted analysis resulted in four trees of 7433 steps and a consistency index of 0.2774. These trees show considerably more agreement among themselves than do the equally weighted trees, resulting in a more resolved strict consensus tree (Fig. 2). In the Bayesian analyses, log likelihood values reached a stable equilibrium well before 200,000 generations. Thus, we chose a burn-in value of 2000 samples and constructed a majority rule consensus tree using the remaining samples (Fig. 3). The trees resulting from the two parsimony analyses and the Bayesian analysis agree in many of the relationships among taxa; however, they also show some differences. We used an S-H test (Shimodaira and Hasegawa 1999, Goldman 2000) to compare the likelihood of each of the 183 trees that resulted from our different methods. Using this method, not surprisingly, the Bayesian tree was found to have the highest log-likelihood score (-12239.41). Most of the equally weighted trees (101 of the 178 trees) had significantly lower likelihood scores than the Bayesian tree ($P < 0.05$). However, none of the 7:1 trees were significantly different from the Bayesian tree ($P < 0.05$). Given the effects of saturation, the Bayesian tree and 7:1 trees are probably better representations of the higher-level relationships among these species than the equally weighted trees.

Parulidae, as currently defined (American Ornithologists' Union 1998), is not monophyletic in any of the trees (Figs. 1–3). Specifically, three warbler taxa were more closely related to tanagers included in the data set than they were to other warblers. The Hispaniolan endemics *Microligea* and *Xenoligea* form a clade with the Hispaniolan tanager *Phaenicophilus palmarum*. This clade was recovered in all analyses and received moderate bootstrap support (61% and 84%) and had a high posterior probability (100%). The Cuban endemic, *Teretistris fernandinae,* was placed as the sister taxon of tanager *Spindalis zena* in the 7:1 weighted parsimony analysis and the Bayesian analysis, but not in the equally weighted parsimony tree. The relationship between *Teretistris* and *Spindalis* had low support and could be the result of long-branch attraction. The Yellow-breasted Chat (*Icteria virens*) was the most basal member of a clade consisting of all remaining warblers in the 7:1 tree and the Bayesian tree. In the equally weighted tree, Yellow-breasted Chat together with Worm-eating Warbler (*Helmitheros vermivorus*) formed the sister taxa to the remaining warblers.

In addition to the non-monophyly of Parulidae, many other clades recovered in this study also do not agree with current taxonomy. For example, the following genera were not monophyletic: *Dendroica*, *Seiurus*, *Vermivora*, *Wilsonia*, and *Parula*. However, large subsets of *Dendroica* and *Vermivora* were found to be monophyletic. In addition, the genera *Basileuterus*, *Geothlypis*, *Oporornis*, and *Myioborus* were monophyletic in all analyses in this study. However, only a few species were sampled from each of these genera.

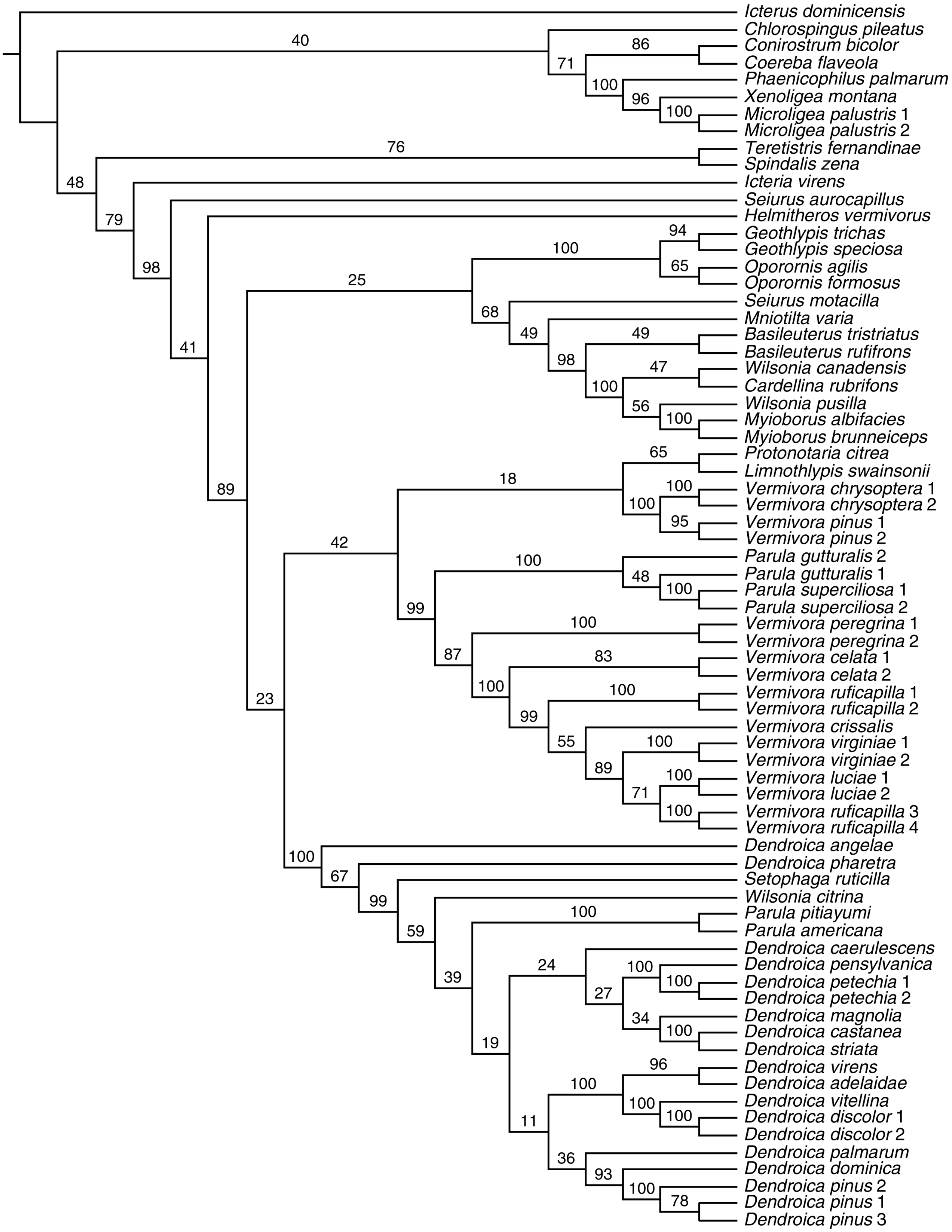

Fig. 1. Strict consensus tree of the 178 most parsimonious trees resulting from the equally weighted analysis. Tree is rooted with *Icterus dominicensis*. Numbers on tree indicate levels of bootstrap support for nodes retained by more than 50% of bootstrap replicates.

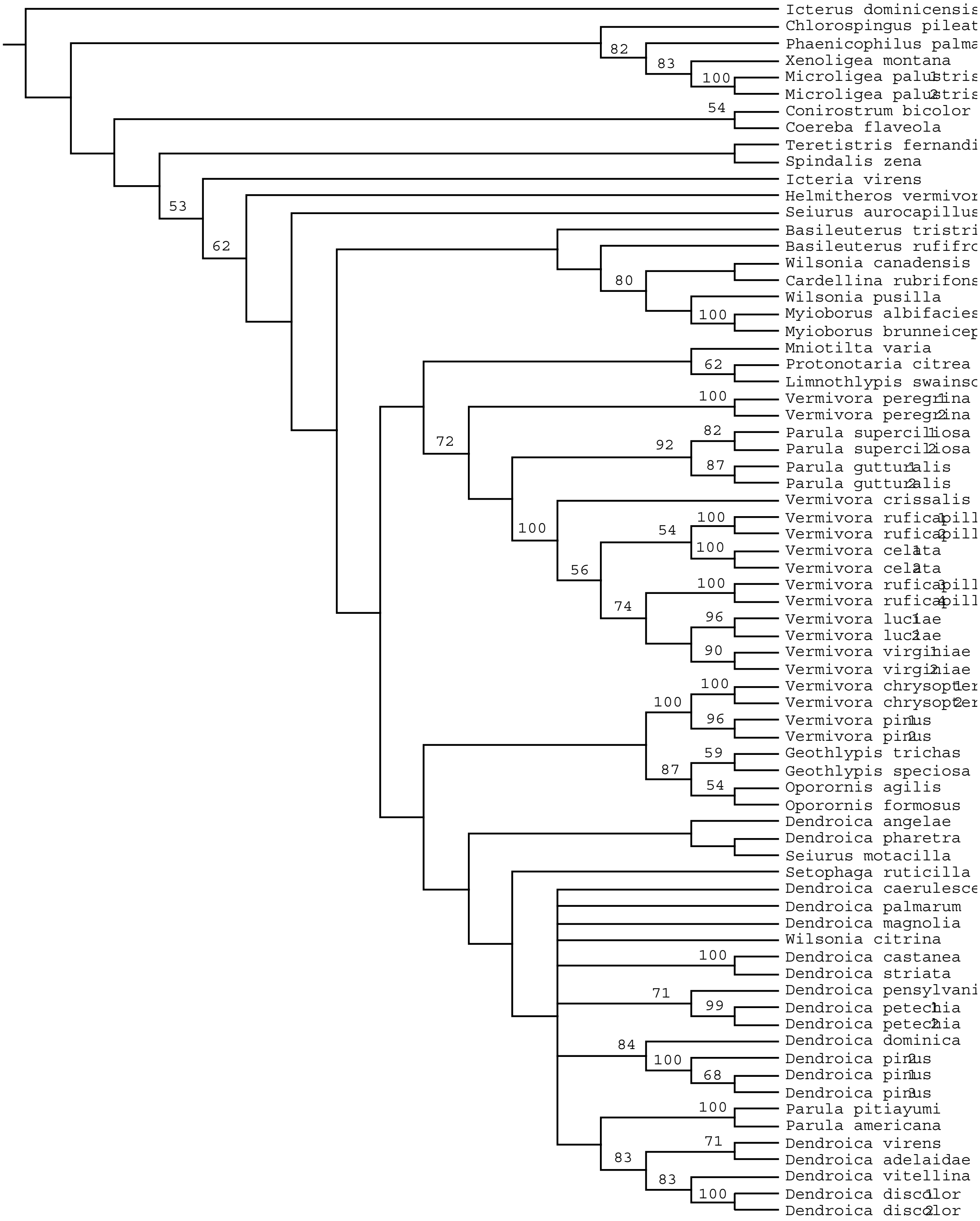

Fig. 2. Strict consensus tree of the four most parsimonious trees resulting from the transversion-weighted analysis. Tree is rooted with *Icterus dominicensis*. Numbers on tree indicate levels of bootstrap support for nodes retained by more than 50% of bootstrap replicates.

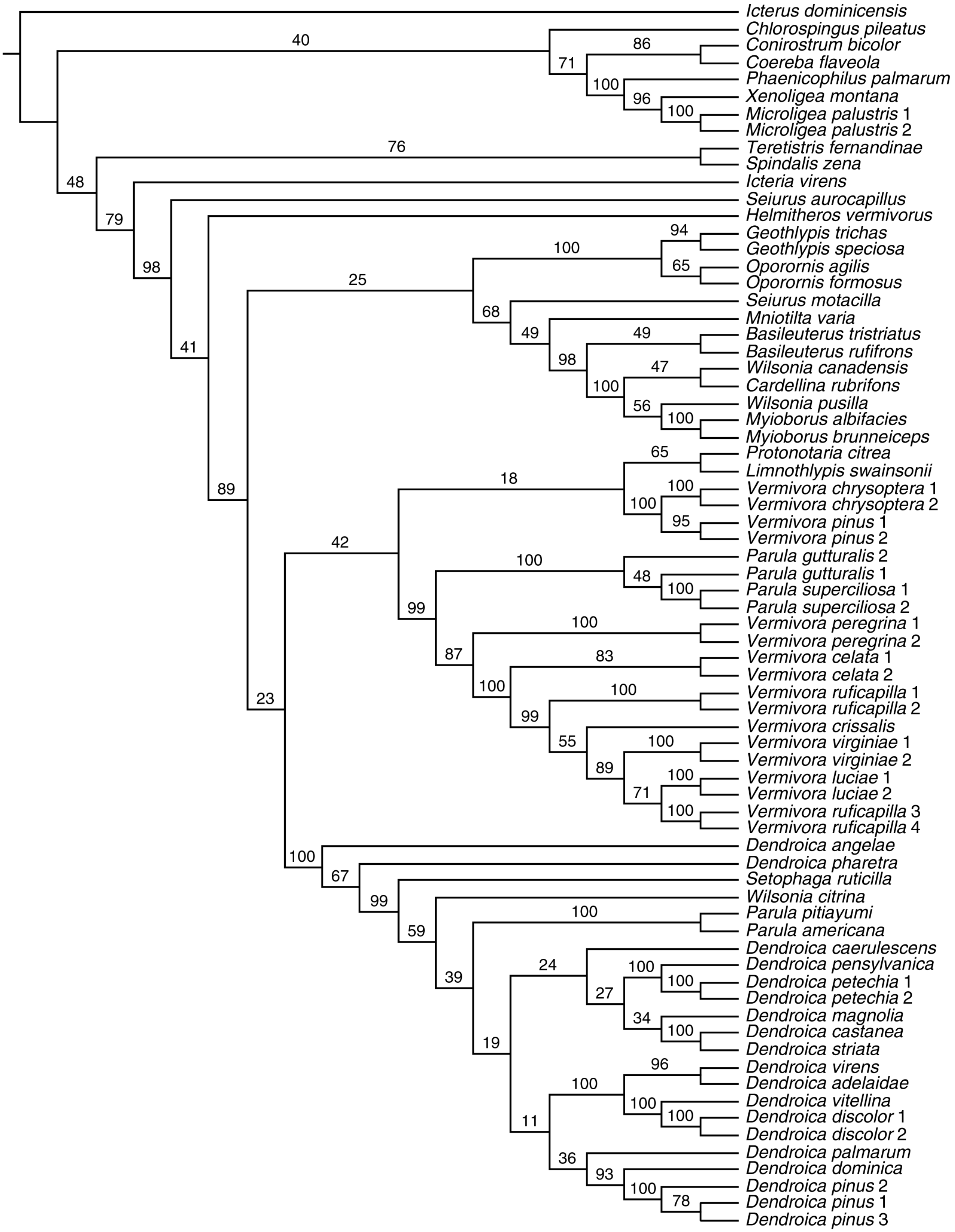

Fig. 3. Majority rule consensus tree of the 8000 trees resulting from the Bayesian analysis. Numbers at nodes indicate the posterior probability of a particular clade.

DISCUSSION

Phylogenetic and taxonomic conclusions

***Non-monophyly of Parulidae.*—**Even though not all genera have been included, results of the cytochrome *b* analysis clearly indicate that Parulidae, as currently defined, is not monophyletic. It is highly unlikely that this conclusion would change with addition of the remaining genera because there is such strong support for the exclusion of *Teretistris, Microligea,* and *Xenoligea* from Parulidae. To make Parulidae monophyletic requires 213 extra steps (2.9% longer) in the transition-downweighted analysis, and 55 extra steps (2.3% longer) in the equally weighted analysis. In both cases the trees constrained to make Parulidae monophyletic are significantly different from the shortest trees ($P < 0.005$). If anything, some of the genera currently classified as parulids but not included in this study (e.g., *Granatellus* and *Zeledonia*) may also end up falling outside of Parulidae. The conclusion of non-monophyly could also be drawn from the analysis of myological data (Raikow 1978), although that study included very few parulids. In contrast, the DNA-DNA hybridization studies (Bledsoe 1988, Sibley and Ahlquist 1990) revealed parulid monophyly, but also had limited taxon sampling and did not include the tanager-like species (e.g., *Microligea, Xenoligea*).

***Monophyly of genera.*—**Some of the phylogenetic relationships suggested by this study are congruent with those recovered by other data sets, and with those portrayed by linear classifications (Lowery and Monroe 1968, American Ornithologists' Union 1998), but there are some significant and intriguing differences. Perhaps the most significant is the finding that few of the genera as currently defined in the American Ornithologists' Union Check-list of North American birds (1998) are monophyletic. Although some genera were monophyletic (e.g., *Basileuterus*, *Myioborus*), none of the genera with reasonably extensive sampling was found to be monophyletic. Below we discuss the limits of the genera of warblers as indicated by the trees found in this study.

Vermivora.—With the exception of the extinct *V. bachmani*, all members of this genus were included in the study. In all trees, *Vermivora* as currently defined is polyphyletic and includes two well-supported clades (Figs. 1–3). One of these clades consists of two species known to hybridize, Blue-winged (*V. pinus*) and Golden-winged (*V. chrysoptera*) warblers. The close relationship of these two species is indicated by high bootstrap support and a high posterior probability (all values 100%; Figs. 1–3). The second clade consists of several mostly southwestern taxa (*V. ruficapilla*, *V. luciae, V. virginiae*, *V. crissalis*, and *V. celata*). This clade also has 100% bootstrap support and 100% posterior probability. In addition, these species show very little genetic divergence from each other. Average sequence divergence between species in this southwestern *Vermivora* clade is 2.0%. In the Bayesian tree, the Tennessee Warbler (*Vermivora peregrina*) is the sister taxon of the southwestern *Vermivora*, but the parsimony trees are not resolved with respect to the position of *V. peregrina*. In all of the trees, the Blue-winged/Golden-winged clade is more closely related to the other genera of warblers than they are to the other *Vermivora*. However, two species of Central American warblers (*P. superciliosa* and *P. gutturalis*) appear to be closely related to the southwestern *Vermivora* and the Tennessee Warbler. These species form a clade in 72% of the 7:1 bootstraps and have a posterior probability of 99%. Although currently classified as *Parula* (American Ornithologists' Union 1998), these two species are sometimes placed in *Vermivora* (Lowery and Monroe 1968).

Within *Vermivora*, Nashville Warbler (*V. ruficapilla*) is not monophyletic. The western samples included in this study are more closely related to Lucy's and Virginia's Warblers (*V. luciae* and *V. virginiae*) than they are to the eastern samples of Nashville Warbler. We can think of three possible explanations for this. Our gene tree based on mitochondrial DNA may not actually reflect the relationships among the species due to incomplete lineage sorting (Pamilo and Nei 1988). Another possibility is recent introgression between *V. luciae*, *V. virginiae*, and western *V. ruficapilla*. Alternatively, our phylogeny may reflect the true relationships among these taxa. *Vermivora luciae* and *V. virginiae* may have split recently from western populations of *V. ruficapilla*. Subsequently, the western populations may have retained similar plumage to eastern populations. Additional genetic markers and additional samples need to be sequenced to evaluate the likelihood of these different hypotheses. Nevertheless, this example is a good illustration of the importance of including multiple individuals of a particular taxon in a systematic study.

Parula.—All four species of the genus *Parula* were included in this study. As mentioned above, two species of *Parula* (*P. superciliosa* and *P. gutturalis*) are more closely related to species within the genus *Vermivora* than they are to other members of *Parula*. This is consistent with the alternative classifications that place these two species in the genus *Vermivora*. The other two species in this genus, Tropical and Northern Parulas (*P. pitiayumi* and *P. americana*) form a strongly supported, monophyletic group (Figs. 1–3). These two species are more closely related to members of the genus *Dendroica* than they are to *P. superciliosa* and *P. gutturalis*.

Wilsonia.—All three species of *Wilsonia* were included in this study, and these species do not form a monophyletic group in any of the trees (Figs. 1–3). The Hooded Warbler (*W. citrina*) is closely related to species within the genus *Dendroica*. Wilson's Warbler (*W. pusilla*) and Canada Warbler (*W. canadensis*) form a monophyletic group with *Myioborus* and *Cardellina*. This clade is closely related to *Basileuterus*. The close relationships between *W. pusilla* and *W. canadensis* to *Myioborus* and *Basileuterus* is supported by at least superficial plumage similarities. Although *W. citrina* was the only species of *Wilsonia* included in the allozyme analysis of Avise *et al*. (1980), it was similarly grouped with *Dendroica* species.

Setophaga.—This monotypic genus has traditionally been maintained to highlight the morphological distinctiveness of the American Redstart's broad, flat bill and prominent, long rictal bristles. However, analyses of behavior and singing patterns (Ficken and Ficken 1965, Parkes 1961, Spector 1992), and of plumage characters (Mayr and Short 1970) suggest that *S. ruticilla* is just a morphologically unusual *Dendroica*. Our trees (Figs. 1–3) agree with this assessment and place *Setophaga* near the base of the *Dendroica* clade. As suggested by Ficken and Ficken (1965), the unique bill and bristle features of *Setophaga* appear to be adaptations to flycatching behavior and thus may actually mask an underlying close evolutionary relationship to the species with thinner bills and shorter rictal bristles that are currently recognized as *Dendroica*. Close relationships among birds of vastly different bill types have been reported in other nine-primaried oscines (Burns 1997, Burns *et al*. 2002). Our placement of *Setophaga* is also supported by the allozyme analysis of Avise *et al*. (1980). An additional mtDNA sequence analysis that included more *Dendroica* species but fewer parulid genera (Lovette and Bermingham 1999) also supports the position of *S. ruticilla* in a clade with *Dendroica*, although its placement within *Dendroica* (whether more basal or more internal) varied with the algorithm used to generate trees.

Seiurus.—This genus currently consists of three species, Ovenbird (*S. auricapillus*), Louisiana Waterthrush (*S. motacilla*), and Northern Waterthrush (*S. noveboracensis*), two of which are included in this study. *Seiurus auricapillus* and *S. motacilla* are not monophyletic in our mtDNA trees (Figs. 1–3). As in the allozyme study of Avise *et al*. (1980), our study placed *S. auricapillus* near the base of the warbler clade. Our analyses disagreed on the placement of *S. motacilla*. Although the 7:1 weighted tree indicates that *S. motacilla* is closely related to some *Dendroica* species, this relationship is not strongly supported. Other trees place this species near the genera *Mniotilta*, *Basileuterus*, *Wilsonia*, *Cardellina*, and *Myioborus*. Data are needed from the third species of *Seiurus* before strong conclusions can be made about the placement of *S. motacilla*. Although strong support for its relationship to other species was not identified, it was not closely related to *S. auricapillus* in any of the trees of this study. The characteristics previously cited as supporting a monophyletic *Seiurus* (e.g., streaked plumage on undersides, lack of rictal bristles; Ridgway 1902, Griscom and Sprunt 1957) could realistically be considered convergent adaptations to the terrestrial lifestyle typical of the three species of *Seiurus*.

Dendroica.—Fifteen of the 27 species in this genus were included in this study. Our trees indicated that *Dendroica*, as currently defined, is paraphyletic. *Parula americana*, *P. pitiayumi*, and *Setophaga ruticilla* are all members of a clade that also contained all of the *Dendroica* included in this study. These species share plumage features (wing bars and tail spots) with *Dendroica*. Additionally, similarities in courtship and singing behavior have also been cited as supporting evidence of the close relationship among these species. Given the evidence from morphology, behavior, and DNA sequences, we recommend that *P. americana*, *P. pitiayumi*, *S. ruticilla*, and all species currently in *Dendroica* be placed in a single genus.

Icteria.—Because the Yellow-breasted Chat (*Icteria virens*) has many aberrant features (Clark 1974, Ficken and Ficken 1962b), the taxonomic placement (familial affinity) of this monotypic genus has been problematic since its initial description. However, Ridgway (1902) stated that its placement in the same higher taxonomic grouping with wood warblers was justified based on its similarities to the parulid taxa *Geothlypis poliocephala* and *Granatellus* spp. (for dissenting opinions see Eisenmann 1962, Ficken and Ficken 1962a, and Mayr and Short 1970). An analysis of appendicular myology in the nine-primaried oscines (Raikow 1978) revealed the presence in *Icteria* of musculature characters shared with other parulids (along with *Coereba* and *Conirostrum*). Although taxon sampling was limited, DNA-DNA hybridization data revealed a basal placement of *Icteria* in Parulidae (Sibley and Ahlquist 1982, 1990), as did a phenetic analysis of allozymes by Avise *et al*. (1980). All trees of this study (Figs. 1–3) place it at the base of a parulid clade. Bootstrap support and posterior probabilities are high, but not overwhelmingly strong for this arrangement.

Historical biogeography in the West Indies

The West Indies as an area of endemism and source of currently more widespread groups of birds.—Most discussions of the historical biogeography of the Caribbean avifauna assume that birds colonized the islands by over-water dispersal. However, Rosen (1976) proposed a vicariance explanation for West Indian organisms. Neithe vicariance nor dispersal hypothesis has to date been rigorously tested for birds. Given the geological history of the Greater Antilles and movement of the Caribbean Plate, vicariance is a viable explanation for faunal distributions on those islands. That the Lesser Antilles were colonized by over-water dispersal is not an issue because these islands are volcanic in origin and truly oceanic (never connected to the mainland). Klein and Brown (1994) provided evidence that some of the Lesser Antilles were colonized more than once by one species, and that the archipelago itself was colonized multiple times by this same species. However, results from that study could not be used to discriminate between vicariance and dispersal hypotheses for the Greater Antilles.

The purpose of the present study is not to discriminate among these hypotheses. However, relationships depicted here can be added to the growing evidence that the West Indies contain not merely a "waif" fauna of species that managed to either arrive by dispersal or be retained after vicariant events. Instead, there is growing evidence that morphologically divergent species found in this region actually represent previously unrecognized adaptive radiations. For example, in the current study, we identified a monophyletic clade containing the "tanager" *Phaenicophilus* and the "warblers" *Microligea* and *Xenoligea*. In Burns (1997), a close relationship was also identified among one of these species, *Phaenicophilus*, and the "tanagers" *Spindalis* and *Nesospingus*. This suggests that all of these taxa form an endemic Caribbean radiation of birds that can not be classified with either the tanagers or the warblers. All of these taxa need to be included in a single analysis along with a variety of tanagers and warblers before definitive conclusions can be made. Nevertheless, our data suggest that the West Indies appear to have played a central role in the diversification of this group of birds. A recent analysis of phylogenetic relationships among Darwin's finches and relatives (Burns *et al*. 2002) mirrors the results presented here. Burns *et al*. (2002) show that the Darwin's finches are derived from a clade of mostly Caribbean birds. Previously, the species in this group were not thought to be closely related and traditionally classified as Emberizidae, Thraupidae, and Coerebidae. Thus, the Darwin's finches may have had their origin in the West Indies, with Caribbean endemics undergoing adaptive radiation and speciation in parallel.

Although a West Indian origin probably does not apply for the Parulidae as a family, some of the clades within the higher taxonomic group probably originated in the West Indies. In both this study and that of Lovette and Bermingham (1999), the most basal members of the clade of *Dendroica* warblers (and genera not currently classified as *Dendroica*, see above) are West Indian endemics (*D. angelae*, *D. pharetra*, *D. plumbea*, and *Catharopeza*). Similarly, relationships within the more recent clade of *D. discolor* and *D. vitellina* illustrate that *vitellina* is the older taxon. Although not all members of the Black-throated Green Warbler complex were included in this study, one of these (*D. virens*) and another Caribbean endemic (*D. adelaidae*) were basal to the *vitellina-discolor* clade. In Lovette and Bermingham (1999), which included most of the *D. virens* species group, *adelaidae* was the most basal member of that group. However, their analysis did not include *D. vitellina*.

Intra-island differentiation and adaptive radiation on Hispaniola.—Although intra-island adaptive radiations are well described for the avifaunas of the Galapagos and Hawaiian islands, such radiations have not been proposed for any of the West Indian avifauna. Intra-island radiations have been well documented in other groups (e.g., anoles —Losos *et al*. 1998; ants — Wilson 1985; *Eleutherodactylus* frogs — Hedges 1989), but discussions of the evolutionary history of birds in this region have not included the role of intra-island adaptive radiation. In this study, we identify a monophyletic group of birds, all of which are endemic to the island of Hispaniola. This well-supported clade includes Black-crowned Palm-Tanager (*Phaenicophilus palmarum*), Green-tailed Warbler (*Microligea palustris*), and White-winged Warbler (*Xenoligea montana*). Our data are consistent with the shared plumage and morphological characteristics of these species (McDonald 1988; R. Storer, pers. comm.).

This evidence of adaptive radiation *within* a Caribbean island has important implications for understanding historical biogeography of the Caribbean region, as well as for understanding the evolution of birds on islands in general. In attempting to provide a general explanation for biogeographic patterns in the West Indies, Ricklefs and Cox (1972, 1978) argued for the presence of a taxon cycle in which, after initial colonization, taxa are widespread and undifferentiated. As time goes on, competition with other species results in their becoming more and more specialized with subsequent range reductions. The ultimate stage is single-island endemism. If such a taxon cycle exists, then single-island endemics should each be on their own evolutionary trajectory with respect to other such endemics in the West Indies; i.e., each represents a relic of a formerly widespread species. This model ignores the strong possibility of adaptive radiation and lack of dispersal to other islands. The results presented here suggest that the assumption of single-island endemics having formerly been more widespread does not apply to at least some of the Hispaniolan endemic birds. Since these three species are each others' closest relatives, it is highly unlikely they each were formerly more widespread and ended up as relics on the same island. A much simpler explanation is that they evolved *in situ* and never dispersed to other islands.

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